Storm effects on intertidal invertebrates: increased beta diversity of few individuals and species

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Short title: Storm effects on intertidal invertebrates

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Abstract

Climate change is predicted to lead to more extreme weather events, including changes to storm frequency, size and location. Yet, the ecological responses to storms are incompletely understood for sedimentary shorelines, the most widespread land-ocean interface. Here we document how four storms of different magnitude impacted the invertebrate assemblages on a tidal flat in Brazil. We specifically tested the relationships between wave energy and spatial heterogeneity, both for habitat properties and faunal descriptors, predicting that larger storms redistribute sediments and hence lead to spatially less variable faunal assemblages. Significantly fewer species at a significantly lower density occurred within days to weeks after storms, which appeared to recover within months. The sediment matrix tended to become less heterogeneous across the flat, but, contrary to expectations, faunal beta-diversity increased after storms. This higher beta diversity was primarily driven by species losses. Changing storm properties may propagate to future changes in ecological process on sandy beaches, possibly impairing provision of ecosystem services. Thus, identifying features that determine resilience and recovery of ecosystem functions shall be a research priority.

Keywords: sandy beaches; beta diversity; benthos; soft-bottom; extreme events; habitat heterogeneity; Araçá Bay

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1. Introduction

Extreme weather events, including changes to storm frequency and intensity, are predicted to increase over the 21st century (IPCC 2013, Lin and Emanuel 2016, Walsh et al. 2016). These global changes to the ecosystem physical and chemical conditions and forcing are having numerous and widespread biological impacts in the sea and on land (Weatherdon et al. 2016). In the global oceans, climate change is modelled to substantially alter the provision of ecosystem services critical to humankind (Gattuso et al. 2015), but many responses in marine ecoystem still remain incompletely understood (Hauser et al. 2016, Nagelkerken and Munday 2016).

Storms may cause massive changes to coastal environments, particularly on sedimentary shorelines, often causing the translocation of sediment from the subaerial beach and dunes, and the landwards movement of the coastline (Masselink et al. 2016). These large habitat changes are usually accompanied by impacts to faunal assemblages, best documented for benthic invertebrates (Jaramillo et al. 1987, Lucrezi et al. 2010,). Mateo and García-Rubiés, 2012

The unpredictable nature of storms generally precludes rigorous experimental designs specifically testing the effects, meaning that nearly all published ‘storm studies’ are largely opportunistic (Harris et al. 2011). In addition, often only a few or no data points are available immediately before a storm, post-storm sampling can be truncated, and for large storms it is challenging or impossible to find control areas that were not affected by the event (Posey et al. 1996); arguably, this makes attribution of ecological patterns to storm effects somewhat weak. An alternative is to make *a priori* predictive hypotheses based on knowledge of the biology of species and their likely response to large disturbance events in their habitat (Harris et al. 2011).

Here, we combine oceanographic, sediment and biological data to investigate how storms can affect the sedimentary habitat of a tidal flat in Southeast Brazil, as well as the associated macrobenthic assemblages. Specifically, we tested four complementary, predictive hypotheses:

1. Higher wave energy during storms may translocate and disperse large sediment volumes , resulting in lower habitat heterogeneity.
2. Reduced habitat heterogeneity may propagate to lower fauna beta diversity.
3. Disturbance caused by storms may reduce the species number , density and biomass.
4. Changes in beta diversity associated with storms may be mainly attributable to species losses rather than replacement.

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2. Material and Methods

2.1 Study area

This study was done on the intertidal flats of Araçá Bay (Brazil, 23° 49'S, 45° 24'W; Figure 1), relatively small bay (ca. 750 m wide and long), which is protected from the prevailing swell by São Sebastião island (Fig. 1). The bay is subject to physical forcing by frontal systems, when current speed may increase eightfold (Fo 1990).

2.2 Field sampling

Thirty four sites were sampled on four times at ca. three month intervals: 25 September 2011, 5 February 2012, 7 May 2012, and 29 July 2012. Sampling sites were selected to a) encompass habitat diversity (i.e. different sediment types and depths), and b) achieve a reasonable spatial coverage (Figure 1). The same locations (+/- 1 m) were sampled during each sampling date by collecting three faunal samples (corer: 20 cm inner diameter, 20 cm depth) and one smaller sediment core (3 cm inner diameter, 20 cm deep).

Three storm events occurred during the study (22 November 2011, 06 May 2012, 18 July 2012; Fig. 2), all accompanied by torrential rain, strong winds, flooding, and building damage. We sampled on the first spring tide after the storms in May and July 2012 (one day lag in May and 11 days in July).

2.2 Biological and environmental data

Faunal cores were washed on the same day through a 0.3 mm mesh sieve, and the retained fauna was fixed in 70% ethanol. Sediment samples were dry-sieved to determine granulometry. Organic matter content was determined by weight loses of dried samples (60°C for 24) after incineration(550°C for 6 h). Calcium carbonate content was determined by 10% HCl digestion.

Sediment temperature and interstitial water salinity were measured *in situ* with a digital thermometer and a refractometer. Wave height and period for the region were obtained for 24.5 S and 45.5 W from the global wave generation model WaveWatch III (NCEP/NOAA). Wave power (as waves' force to disturb the benthos) was calculated as (P_w) as: $P_w = \rho g^2 H^2 T / 32\pi$, where ρ is water density (1,027 kg/m^3), g the acceleration due to gravity (9.81 m/s^2), H the wave height (m), and T the wave period (s) (Herbich 2000). All activities complied with the license from the appropriate federal environmental agency (*Ministério do Meio Ambiente (MMA)* – *Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio)* No. 19887-1; acronyms for, in English: Ministry of the Environment – Chico Mendes Biodiversity Conservation Institute).

2.3 Data analysis

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We tested for differences in habitat heterogeneity and fauna beta diversity amongst times with permutational analysis of multivariate dispersion (PERMDISP, Anderson 2006) based on Euclidean distances and normalized sediment data (habitat heterogeneity) and Bray-Curtis dissimilarity and the abundance data for the full suite of species (fauna beta diversity).

We tested for differences in total abundance, biomass, and species richness amongst times using general linear models with 'Time' as fixed factor, based on negative binomial distributions for count data and gamma distributions for continuous data. Differences among sampling times were compared by Tukey post-hoc tests using the MASS package in R.

We used the beta diversity partitioning framework (Podani and Schmera 2011; Carvalho et al. 2012) to investigate compositional changes of macrobenthos over time. It partitions compositional differences among communities (β_{total}) into β diversity attributed to species replacement (β_{repl}) and β diversity attributed to species loss or gain (β_{rich}). This analysis was done with the R package BAT (Cardoso et al. 2015)

3. Results

H1: Lower habitat heterogeneity after storms

Sediment properties were spatially more homogeneous after periods of higher wave power, but differences between sampling times were not significant (Fig. 3a; PERMDISP P = 0.586).

H2: Beta diversity declines after storms due to more homogenous sediment matrix.

Macrobenthic assemblages showed a significantly higher β diversity following periods of higher wave power (Fig. 3b; PERMDISP P = 0.003).

H3: Storm disturbance results in lower abundance, biomass and species richness

Abundance and species richness were significantly lower in samples taken shortly after high-energy wave events (Fig. 4). The mean number of species per site was significantly lower (i.e. 9.82 species) after the strongest wave event than at other times (i.e. 11.82 to 14.35 species) (Fig. 4a). Abundance peaked at 4126 ind. m^{-2} in Feb. 2012 and showed a significant decline to 1195 ind. m^{-2} after the storm in May 2012 (Fig. 4b). In contrast, total biomass did not change significantly over time (Fig. 4c).

H4: Species losses drive most of the change in beta diversity.

Declines in species numbers accounted for most of temporal beta diversity in the macrobenthos (Table 1). By contrast, species replacement was less important (Table 1).

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4. Discussion

Significant changes in macrobenthic species richness and abundance in a tropical tidal flat were associated with temporal variation in wave energy. This resulted in significant changes of faunal beta diversity over time that was mainly attributable to species losses, but, apparently, unlinked to variation in habitat heterogeneity.

Previous studies about the influence of storms on coastal soft-sediment ecosystems have shown that storms may have stronger impacts on environmental features than on the fauna (Saloman and Naughton 1984, Cochôa et al. 2006) (Alves and Pezzuto 2009, Harris et al. 2011), and that offshore sediment transport is the dominant geo-morphological response of beaches to increased wave energy (Masselink et al. 2016). These studies, however, were mostly done on exposed ocean beaches, habitats with a small species richness that are well adapted to high-energy conditions (Brown 1996, Schlacher et al. 2008). By contrast, our results showed that under more sheltered conditions, storm impacts were more evident in the fauna than in the sediments.

The observed decrease in the number of species and individuals may have been caused by redistribution of sediments, burying fauna at some site and winnowing them at others. These mechanisms are functionally supported by studies showing significant changes of the macrobenthos following sediment deposition and substantial alterations in hydrodynamic regimes (Jaramillo et al. 2012, Cummings et al. 2003, Rodil et al. 2011, Schlacher et al. 2012).

Storms were followed by decreases in the density of normally abundant and widespread species, such as the crustacean *Monokalliapseudes schubarti* (Mañé-Garzón, 1949), the polychaete *Isolda pulchella* Müller in Grube, 1858 and the bivalve *Anomalocardia flexuosa* (Linnaeus, 1767). These species have low mobility, suggesting that endobenthic animals with limited mobility may be more vulnerable to storms than more mobile epibenthic species (Negrello Filho and Lana 2013, Urabe et al. 2013). At Araçá Bay, infaunal species are also essential preys for fish and birds and, also, they are important contributors to local nutrient cycling (Leite et al. 2003, Corte et al. 2014). Thus, storms may also impair ecosystem function in intertidal flats, but this thesis needs to be tested more widely and rigorously.

The observed storm effects on the macrobenthic fauna of Araçá Bay appeared to be stronger, short time after each larger event. We found that differences in environmental and biotic characteristics were most pronounced in May 2012, when samples were taken one day after the storm had passed. There was another storm in November 2011, but no substantial changes before (Sep. 2011) and after (Feb. 2012) this event, suggesting that storm recovery may occur within months, or even shorter, in this particular system.

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The fauna of sandy beaches generally shows clear and quick responses (e.g. altered diversity and assemblage composition) to short-term changes in hydrodynamic forces (Schlacher and Thompson 2013). Likewise, most species typical of coastal sedimentary ecosystems are, to some degree, adapted to high-energy conditions and hence may recover relatively quickly (e.g. within days to weeks) from most storm events (Gallucci and Netto 2004, Harris et al. 2011, Machado et al. 2016). For example, Negrello Filho and Lana (2013) did not detect significant storm effects on macrofaunal species richness and abundance after 5-8 days in an estuarine system. Similarly, Machado et al. (2016) found recovery of macrobenthic assemblages inhabiting ocean exposed beaches within seven weeks of a storm. It is important to emphasize, however, that recovery depends on the magnitude, spatial scale and return frequency of the disturbance events in sandy beaches and other marine systems (Urabe et al. 2013, McClain and Schlacher 2015). The most powerful storms may cause ecological changes that require years to recover (Jaramillo et al. 1987).

The timing of a storm in relation to the tidal regime is also important in determining ecological impacts. Masselink et al. (2016) found that storms impacts on the south-west coast of England were highest when the peak storm waves coincided with spring high tides. In our study, this was likely the case in May 2012 when the height of the storm passed during a spring tide.

Here we show that storms can cause significant changes to macrobenthic assemblages inhabiting a tidal flat. In terms of abundance and diversity, the fauna appeared to recover within a few days, while an increased beta diversity persisted beyond that. Given that storm activity, location and intensity are predicted to change over the coming decades in a warming world (Lin and Emanuel 2016, Walsh et al. 2016), ecological changes attributed to altered storm properties are likely expected. However, the functional consequences of altered storm regimes for the ocean's sandy beaches are fundamentally unknown, including the continued provision of ecosystem services to coastal communities and beyond. Thus, future work shall prioritise investigations of how ecological processes in ocean beaches respond to extreme events and which features may determine the resilience of beach ecosystems and their recovery.

Acknowledgements

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Table 1 – Beta diversity and beta diversity partitioning among sampling periods. Higher values of beta diversity denote greater differences in the composition of species and number of individuals between two consecutive sampling times.

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	Total β diversity (βtotal)	**Species replacement / substitution (βrepl)**	**Species loss / gain richness differences (βrich)**
Sep. vs Feb.	0.45	44.4%	56.4%
Feb. vs May	0.79	16.4 %	83.6 %
May vs July	0.47	11.7 %	89.3 %
mean	0.57	24.2 %	76.4 %

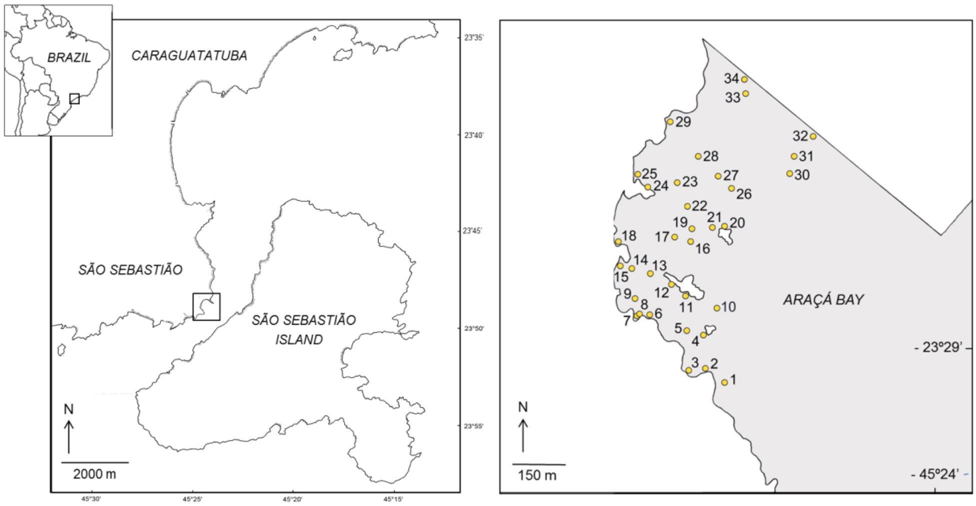

Fig. 1 Map showing the location of the study area (left panel) and the sampling sites in the intertidal area of Araçá Bay (right panel).

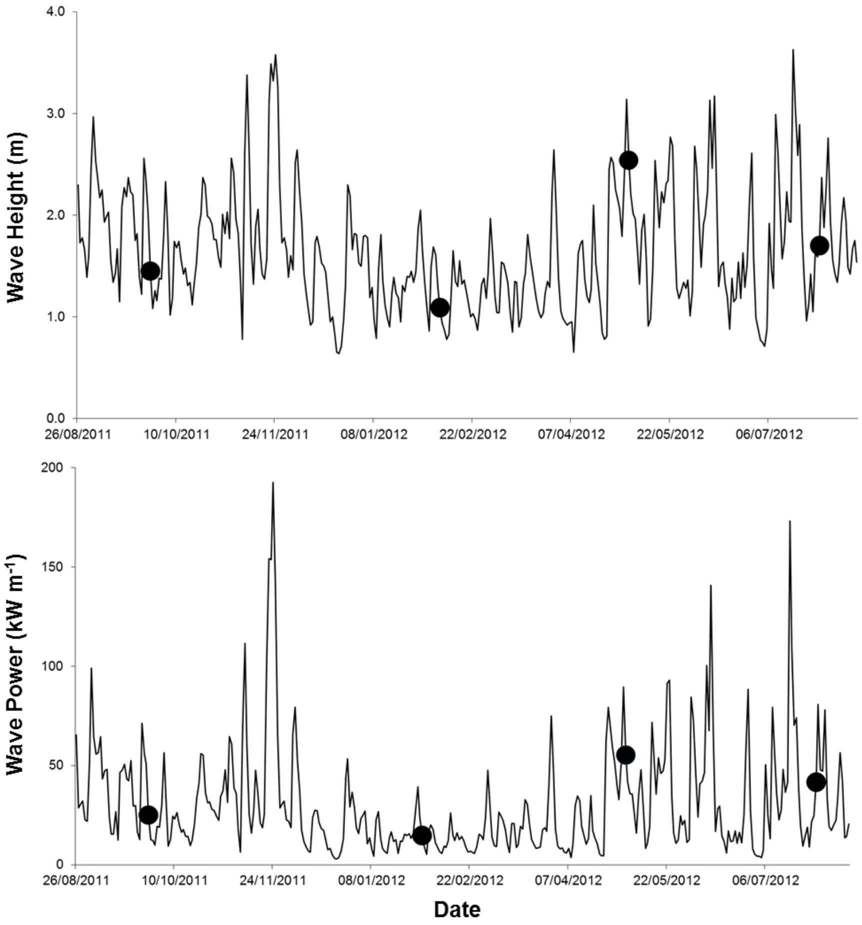

Fig. 2 Wave height and wave power during the study period (sampling events are shown by dots).

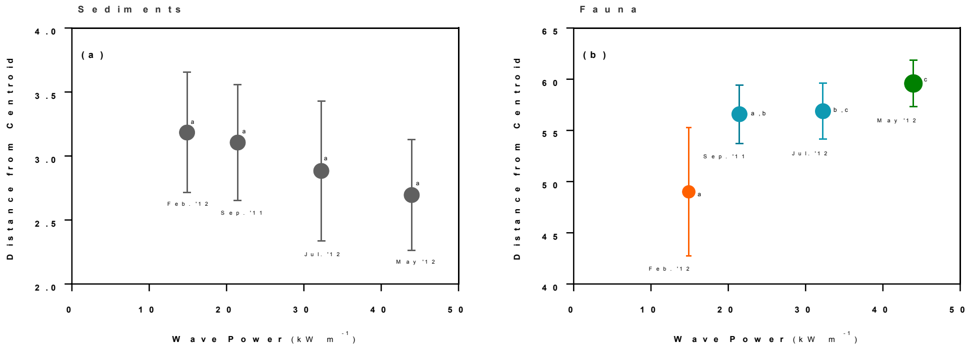

Fig. 3 Beta diversity of a) habitat properties and b) macrobenthic invertebrates among sites at four sampling events associated with significant variation in wave energy preceding each event. Measure of beta diversity is the distance from centroids across all sites at a time. Letters and colours denote homogenous groups in generalized linear models. Error bars are 95% confidence intervals.

Comentario [18]: this should be better explained in methods

Fig. 4

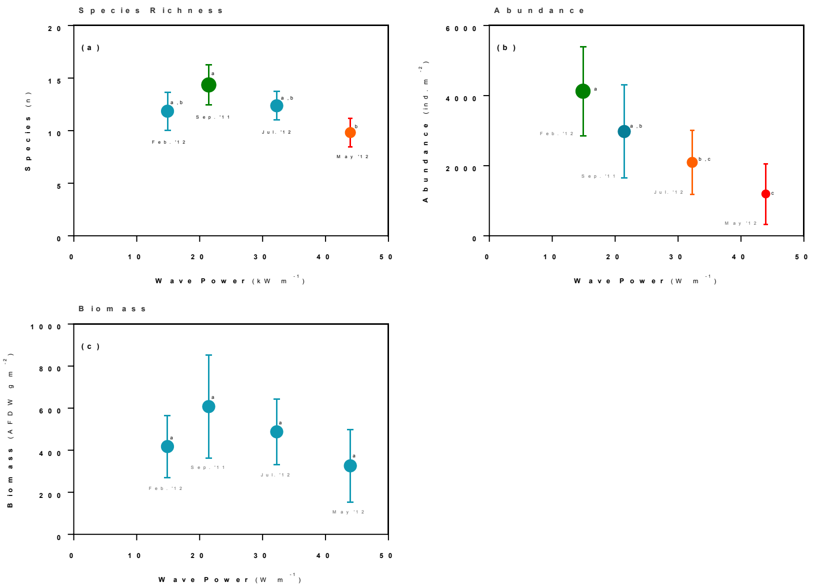

Fig. 4 Variation in the mean number of species per site (a), total abundance (b) and total biomass (c) of macrobenthic invertebrates at four sampling events associated with significant variation in wave energy preceding each event. Letters and colours denote homogenous groups in generalized linear models. Error bars are 95% confidence intervals.